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Influence of Climate on the Distribution of Walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from Thermoregulatory Behavior.

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(Plates I-IV; Text-figures 1-2)

Introduction

THE walrus is one of a group of pinnipeds typically associated with the ice front in northern seas, but like most of the others, it is by no means restricted to the front. Some walruses occur as much as 1,000 miles south of it in summer and some as much as 500 miles north of it in winter. Within this range, the walrus resides chiefly in the shallow waters of the continental shelf, where its food of mollusks and other benthic invertebrates is obtained at depths of 80 meters or less (Vibe, 1950). The area occupied by these mammals on a year-round basis thus comprises parts of two marine zoogeographic zones, the Arctic and the Boreal or subarctic (Ekman, 1953; Zenkevitch, 1963), but does not include the full extent of shallows in either one. The failure of walruses to occupy all of the shoals and inshore waters of the Arctic Zone seems to be clearly a matter of their inability to penetrate regularly into the polar ice-pack or to obtain food in some areas where mollusks are scarce (Fay, 1957). Their occupation of only the northern part of the Boreal Zone may be due to restrictions imposed by the climate, which varies from subarctic in the northern part to low temperate in the south. A correlation between the southern limit of the walrus' range and isothermal lines was noted more than a century ago by von Baer (1838, *fide* Allen, 1880:91), and we find this to be generally true today. The majority of these animals occurs in areas where monthly mean air temperatures are from −15 to +5°C, and only a few vagrants range south of the 10°C isotherm at any time (Text-fig. 1). In the study reported here, we set out to test the theory of a southern climatic boundary, not by comparing distribution with thermal conditions, but by examining the behavioral and physiological responses of walruses to subarctic and temperate climates. In this paper we report on the behavioral aspects of the study; the physiological findings are reported separately (Ray & Fay, 1968).

The material presented here is of two kinds. First are descriptions of the postures and other physical adjustments of walruses that affect the amount of exposed surface area and could influence the rate of heat loss from the body to the ambient. Second is a quantitative comparison of the weather when the animals were *out* versus *in* the water. Walruses spend about as much time out of the water as in it, and the frequency and duration of their lying out seem to be affected by the weather conditions at the time (Shuldham, 1775, *fide* Allen, 1880:67; Hayes, 1867:404; Nikulin, 1947). Since their presence in or out of the water may depend also on the normal alternation of activity and rest, we have included an investigation of the normal activity rhythm.

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TEXT-FIG. 1. The north polar region, showing the present distribution of walruses in summer in relation to the minimum extent of the permanent ice pack and the isotherm of 10° C mean air temperature for July.

Materials and Methods

Information on the behavior of free-living walruses was obtained mostly by Fay during the period 1952 to 1965, in the vicinity of St. Lawrence Island, Alaska, just south of Bering Strait. In the course of approximately 400 hours spent hunting walruses with the Eskimos of that area, at least 1,190 adults, subadults, and juveniles were seen, plus many calves not included in the counts. More than 8,000 others were seen during aerial surveys of the Bering Sea. Most of these animals were sighted during the daytime, between 0800 and 1600 hours, when more than four-fifths of them were lying out on ice floes; the rest were swimming or feeding in the water. Although the Eskimos' objective during the hunts was to kill the animals for food, observation of undisturbed animals was usually possible for several minutes before the shooting occurred. In that time, behavior of potential thermoregulatory value was observed.

Most of the field observations were made in May, when the Pacific walrus population was

concentrated in the northern end of the Bering Sea. The behavior of the animals in that time and place is assumed to have been representative of their responses to weather slightly warmer than the mean for their year-round environment. Observations in the vicinity of St. Lawrence Island during January to March provided some indications of the reactions to the coldest weather to which walruses are ordinarily exposed in the Bering Sea region; the island is the northern limit of their range at that time (see Brooks, 1954). For observation during the warmest weather in summer, Fay went to Round Island (58° 30′ N, 160° W), Bristol Bay, Alaska, the southernmost area regularly occupied by Pacific walruses in that season. About 1,500 males were observed there during a four-day visit at the end of June, 1958.

The data obtained in the field on the activity rhythm and reactions to weather were mostly notations of the time, location, and number of animals seen *in* (swimming) or *out* (resting) of the water. Only those animals that were undisturbed were counted; alarmed walruses invariably took refuge in the water. These notes were later correlated with meteorological data recorded by us or by personnel of a nearby weather station. The data were biased to the extent that it was usually not possible to observe the animals during periods of extremely stormy weather.

Our information on the behavior of walruses in captivity was obtained from 1957 to 1963, principally by Ray at the New York Aquarium. The animals from which most of the information was obtained were an adolescent male, probably of Greenlandic origin, and a juvenile female from the Bering Sea. Both had been in captivity since infancy. Data on their activity rhythm and reactions to weather were obtained in 1960, during a six-month period of close surveillance. At that time, the male was about five years old, and the female was about one year old. At regular intervals each day, notations were made whether each animal was in the water or hauled out on its resting platform, and these were correlated with hourly weather recorded by the U. S. Weather Bureau, 17 Battery Place, New York City. The weather records were less applicable than on-site micrometeorological data would have been, but the conditions described by them were similar to the general weather at the aquarium. One notable exception to this was wind velocity; winds were stronger and more frequent at the Battery than at the aquarium, and within the sheltering walls of their enclosures the animals were further removed from the effects of all but strong winds.

From January 18 to May 30, notations on activity were made several times daily between 0800 and 1600 hours and, after May 30, also at 0200, 0600, and 2200 hours. At 0800 hours daily, throughout the six-month period, a notation was made also of the presence or absence of feces on each animal's resting platform. Since the animals seldom defecated on the platforms except when they stayed out for an hour or more beforehand, we used this as an index of their having spent some time out of water during the night. In June and July, when both this index and their regular nighttime observations were recorded, they showed close agreement.

The captives were kept in separate, walled enclosures about 20 meters apart and were visually, but not acoustically or olfactorily, isolated from each other. Since vocal communication between them was rarely detected, and since neither animal was sexually mature, we are confident that any intercommunication that did occur did not seriously influence their behavior. The male's enclosure also held three gray seals, *Halichoerus grypus*, but the walrus was dominant over these and virtually unaffected by their presence. Neither did the presence of human spectators seem to distract either animal to the extent that its activity rhythm was affected. Although the spectators were not ignored while the walruses were swimming, the animals were largely oblivious to all human activity when they hauled out to rest. The aquarium was open to the public from 1000 to 1700 hours daily to May 30 and from 1000 to 2200 hours thereafter. The only significant human influences on the behavior of the animals during that time were the daily feedings; each animal usually hauled out on its resting platform when the keeper arrived with the food at 1030 to 1100 hours and 1530 to 1600 hours. Spot observations were recorded at those times each day before feeding.

The juvenile female was one of 21 individuals obtained at St. Lawrence Island between 1958 and 1963. All of these were very young animals when captured, ranging in age from newborn to three or four weeks old. They were held in pens on the island for up to two weeks before being transferred by aircraft to the aquarium. In that time, we obtained information on their reactions to the local weather and, in a few cases, to a wide range of experimentally imposed thermal conditions. Comparative information on their reactions to hot summer weather was obtained after their arrival in New York.

Results

Regulation of Surface Exposure in Air

Four methods were used by walruses to regulate exposure of their body surface and appendages to the ambient while at rest out of water. These were huddling, posture, fanning, and selection of substrates. These will be considered separately, though they often occurred simultaneously.

Huddling. Of nearly 10,000 walruses seen by us from small boats and aircraft, less than three per cent were alone; the rest were in groups of from two to several hundred. The mean size of the groups tended to be smallest when the animals were in the water, larger when they were on ice, and largest when they were on land (Table I). One characteristic of each group resting on ice or land was the intense mutual contact between its members, which lay "... huddling like swine, one over the other" (Cook, 1822:680). This is at once apparent to anyone seeing a resting herd for the first time (Plate I), and it has been mentioned many times previously in accounts by naturalists and other explorers of arctic regions (e.g., see review by Allen, 1880: 107-121, 178-180). In captivity, also, walruses show a high degree of gregariousness and thigmotaxis; when two or more of those that we studied were kept in the same pen, they almost invariably slept huddled together. We estimated that the usual extent of contact in groups, both in the field and in the aquarium, was about 20 per cent of the total body surface per animal.

Table I.
Group Size of Wild Pacific Walruses in Relation to Their Location.[a]

Location	No. of Animals	No. of Groups	No. of Animals per Group: Range	Mean
In water	339	94	1- 50	3
On ice	6274	388	1-600	16
On land	3254	21	1-850	155

[a] From unpublished data obtained by J. W. Brooks, K. W. Kenyon, A. Thayer, and F. H. Fay during aerial surveys and observation from small boats, Bering Sea, 1952 to 1962.

The degree of mutual contact within groups did not appear to vary seasonally, with latitude or with air temperature or other weather conditions. Herds on the beach at Round Island in June, under clear skies and in 14°C air, were apparently as tightly packed as those on the ice in January when the sky was cloudy and air as cold as–19°C. In the aquarium, also, the animals huddled together to sleep, regardless of whether they were cold, warm, or hot; under the warmest conditions, both the wild and the captive animals showed signs of heat stress.

In the field, we observed another type of huddling, characteristic of mother-and-calf pairs, which we called "brooding" in as much as it seemed to be of benefit to the calf alone. In this case, there were distinct variations in the degree of contact that seemed to be adaptively related to the weather. For example, we noticed at first that very few calves were in evidence during the chilliest days, but in sunny weather with little or no wind they were frequently seen standing or lying on the ice beside the mother. Subsequently, we discovered that in cold weather the calf was usually situated against the mother's breast, between her forelimbs, and so completely concealed and sheltered that its presence was not detected until the mother became alarmed and began to flee. Calves in this position were estimated to have at least 50 per cent of their body surface in contact with that of the adult. When removed from this maternal shelter and exposed alone to the chilly weather, the calves reacted by seeking protection from the wind, huddling against any warm body or low-conductance material, assuming a "fetal" position, and shivering violently. They were obviously chilled and we concluded that the warmth derived from maternal brooding was an important and, possibly, essential component of their environment. In our experience, weather severe enough to bring about these responses occurred, on the average, in at least three out of four days during the calving season (April-May), and sometimes lasted for ten days at a time.

Posture and fanning. By varying their posture and the position of their appendages, walruses at rest are capable of controlling the amount of exposed surface area. Maximum exposure is attained by sprawling on the back with head and neck extended and flippers outstretched and spread. Minimum exposure is effected by assuming the "fetal" position, with head drawn in, back arched, and flippers pressed tightly against the body. From comparative photographs of one calf in both positions (Plate II), we estimate that the amount of surface exposed in the fetal posture is only about three-fourths as much as in the sprawling posture. That postural regulation of exposed surface is influenced by ambient temperature was determined experimentally. Four newly captured calves, each in a separate wooden crate, were exposed to an in-

crease of 3 or 4°C every 15 minutes. At the lowest temperature, about 1°C, each animal assumed an extreme fetal position with occasional violent shivering. As the temperature was raised, each became more relaxed and paid less attention to keeping its appendages against the body. At 10°C, the animals became fully relaxed and lay either on the back or side; at 15°C they began to sprawl and extend their appendages; at 18°C they became restless and began fanning intermittently with their flippers; at 20°C they were so restless that the experiment was terminated.

The postural adjustments of isolated wild adults in relation to air temperatures were similar to those of the experimental calves. There was clearly a trend to fetal postures at low temperatures (Plate III, fig. 5) and to sprawling at high temperatures, but it was usual to find a wide variety of postures under the latter conditions (Plate III, fig. 6). We found that the fetal posture was almost always assumed when the animals first emerged from the water and was maintained for some time, even when the air temperature was relatively high. In air warmer than 10°C, the emergent animals usually relaxed to a more or less sprawling position after about 30 minutes, or when their skin became dry. We assume that the change in posture reflected a change in the rate of heat loss per unit of surface, i.e., in relation to evaporative cooling.

Fanning by walruses in the aquarium was often seen when ambient temperatures were higher than 20°C but rarely at lower temperatures. In general, fanning animals were visibly hyperemic and hot to the touch, indicating rapid dissipation of body heat. Fanning and superficial hyperemia were seen also in the herds at Round Island, where they were lying in the sun in 13 to 14°C air (Plate IV, fig. 7). We did not see fanning or hyperemia in animals on the ice, even when air temperatures were as high as 7°C, but J. J. Burns (personal communication) saw fanning by some adult males when the temperature was about 8.5°C (Plate IV, fig. 8).

Selection of substrates. A group of three newly captured calves, held in an outdoor pen with a floor of snow, had access to a 1-meter-square piece of plywood and approximately equal areas of canvas and of fresh skin from an adult walrus. The group elected to sleep huddled on the wood, rather than on the snow or other materials, and their persistent use of it indicated that they found it preferable, perhaps because of its lower conductance and specific heat. Pieces of plywood were then provided to several younger calves in separate pens, and these also were consistently used as beds, in preference to the ice and snow of the pen floor.

A positive response in cold weather to substrates of low conductivity and specific heat was suggested also by the behavior of the captives in New York. When they hauled out to rest in the winter, they clearly avoided snow-covered surfaces, and the female selected a wooden pallet rather than an adjacent concrete platform. The male walrus had only a wooden platform on which to lie.

Probable selection of substrates by free-living walruses was noticed only under the warmest conditions at Round Island. Several times, resting animals were observed to grope about with their hind flippers and, on touching a damp, shaded rock, to press the spread flippers firmly against it, as if aware of its coolness. Although the temperature of the damp rocks in shade was only 1 or 2°C lower than that of the air, they were distinctly cooler to the touch because of their high specific heat and conductivity.

Influence of Weather on Emergence

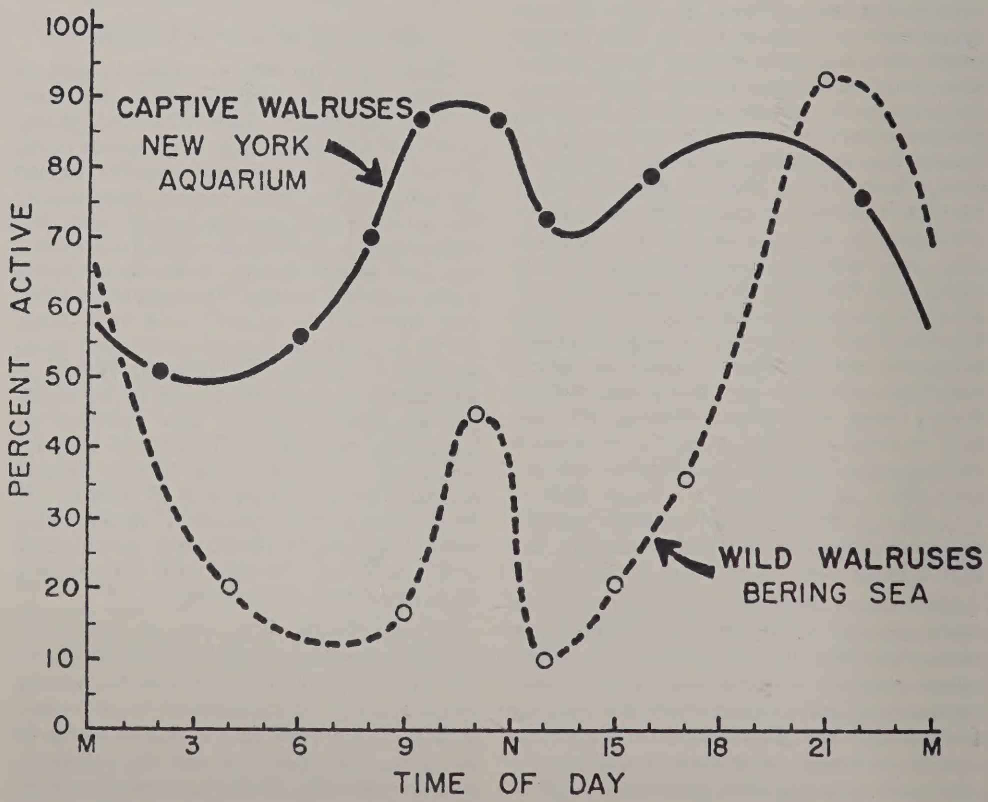
The opinion that walruses prefer to haul out in sunny weather was expressed by Shuldham (1775, *fide* Allen, 1880:67) and Hayes (1867:404), based on their observations of the animals under natural conditions. We formed the same opinion, independently, from our initial nonsystematic observations of both wild and captive animals and noted, furthermore, that they seemed to stay in the water during windy or stormy weather. The latter was noticed also by Nikulin (1947) and Mansfield (1958:115). These opinions were tested quantitatively by means of a sampling system, in which periodic spot-observations of the activities of captive walruses were recorded by impartial observers and correlated with meteorological data, supplied by the Weather Bureau. Inasmuch as the emergence of the animals and the duration of their exposure to weather might be governed also by regular daily and seasonal cycles of activity, the data were analyzed first for evidence of activity rhythms.

Activity rhythm. Other than an opinion expressed by some Eskimos to Loughrey (1959:39) that walruses feed mostly early in the morning and haul out to rest in the remainder of the day, there is no published information available on the normal alternation of rest and activity in these animals. We obtained an estimate of the mean daily activity rhythm of wild walruses by compiling a series of data on several thousand that were sighted in the Bering Sea in the months of January to June, 1952 to 1960 (F. H. Fay,

K. W. Kenyon & A. Thayer, unpublished). A comparable estimate for walruses in captivity was obtained from more than 1,000 spot-observations of the two juveniles in the New York Aquarium, January to July, 1960. Animals sighted in the water were considered to have been "active;" those sighted on land or ice were considered as "inactive." The relative number of active animals per unit of time was found to show a general circadian rhythm in both the natural and the artificial environments (Text-fig. 2). The animals tended to be most active in the forenoon and evening and to haul out most often in early morning and early in the afternoon. The respective proportions of walruses in and out of the water suggested that the wild animals were less active in the daytime and more active at night than were the captives, perhaps because of differences in their feeding times.

We did not detect any significant changes in the mean circadian rhythm per month, from January to July, except in the intensity of activity. In both the wild walruses and those in captivity, more time was spent in the water in January than in any other month (Table II). The wild animals were out of the water most often in February and March, at the height of the mating season (Fay, unpublished); the captives were out most in March and April. From April to July, the captives hauled out with increasing frequency at night and decreasing frequency in the daytime.

Activity in relation to weather: captive walruses. Four kinds of meteorological data were utilized for comparison of the weather when the animals were out of the water (inactive) with that when they were in the water (active). These were: air temperature, sky cover (inversely proportional to insolation), precipitation rate and wind velocity (Table III). Since, in a



TEXT-FIG. 2. Comparative patterns of activity rhythms of wild and captive walruses, based on the percentage of occurrences of animals sighted in the water per hour.

TABLE II.
RELATIVE ACTIVITY OF WALRUSES PER MONTH.

Locality and Time	Jan.	Feb.	Mar.	Apr.	May	June	July
Wild walruses, Bering Sea							
Daytime, total sighted	323	261	10124	4569	5891	648	...
Daytime, per cent active	*77*	*4*	*14*	*22*	*29*	*39*	...
Captive walruses, N.Y. Aquarium ..							
Daytime, total observations	46	103	142	122	136	239	149
Daytime, % when active	*93*	*89*	*74*	*63*	*76*	*79*	*81*
Nighttime, total observations	25	54	57	45	60	59	38
Nighttime, % when active	*76*	*91*	*75*	*62*	*52*	*59*	*47*

TABLE III.
COMPARISON OF MONTHLY MEAN WEATHER WHEN CAPTIVE WALRUSES WERE *out* OF THE WATER WITH THAT WHEN THEY WERE *in* THE WATER.

Month	No. of Observations		Mean Temp. (°C)		Mean Daytime Sky Cover[a]		Mean Precip., mm/hr		Wind, 30 mph or More (% Occur.)	
	Out	In	Out	In	Out	In	Out	In	Out	In
January	3	43	2.1	2.4	83	69[b]	0	.18	0	21
February	11	92	2.2	3.0	81	60[b]	.13	.43[b]	27	38
March	37	105	2.7	0.7[b]	44	58[b]	.13	.80[b]	11	19
April	45	77	11.3	10.9	52	59	:29	.42	11	13
May	33	129	15.2	16.5[b]	56	60	.13	.90	0	8
June	102	259	20.1	21.1[b]	51	56	.62	.51	2	4
July	74	169	21.8	22.3	41	54	.19	2.86	0	2

[a] Expressed as per cent of total sky obscured by clouds; inversely proportional to isolation.
[b] $P < .05$.

preliminary analysis, we found the correlations of activity and weather to be unaffected by the circadian rhythm, all of the data were treated equally. Monthly means were compared by appropriate statistical tests; differences, when $P \leq .05$, were considered as significant. Water temperatures during the six-month period, from mid-January to mid-July, ranged from 4 to 18°C, respectively.

During January and February, the animals stayed in the water most of the time (Table II), and on the few occasions when they did haul out, the weather was slightly cloudier and cooler but less windy than when they were in the water. High winds, 13.4 meters per second (30 mph) or stronger, occurred very frequently in both months and were correlated to a significant degree with the sunniest weather.

March was actually a cooler month than February, though there were more sunny days. The male was out during the day more often than in any other month; the female still remained in the water most of the time. The weather when either of them was out was warmer, sunnier, drier, and less windy than it was when they were in the water. High winds were still correlated with sunny weather, but they occurred less often than in February.

In April, the female was out of the water more often than the male during the day, and this relationship persisted through July. The daytime weather while either of them was out was slightly warmer and sunnier than when they were in the water, but about equally wet and windy.

By May, both animals were out less frequently during the day and more frequently at night. When they were out of the water in the daytime, the weather was slightly sunnier and less windy, but cooler and drier than when they were in the water. In this and the succeeding month, the high winds occurred with cloudy skies.

The tendency toward hauling out less frequently by day and more frequently by night increased through June and July. In both months, the weather when the animals were out

of the water in the daytime was slightly sunnier; in both the day and the night it was less windy but cooler and about as rainy as when they were in the water.

Consistently, throughout the six-month period, the animals tended to avoid exposure to high winds, irrespective of the other conditions at the time. In addition, they showed a negative response to precipitation, especially in the cooler months, and a consistent affinity for sunshine during March to July, i.e., when it was strong enough to have a distinct warming effect. They evidently were not influenced by "trace" amounts of precipitation, but greater amounts were clearly avoided. Precipitation of 0.5 mm/hr or more occurred about three times more often when they were in the water than when they were out. Neither animal was out of the water in precipitation greater than 0.5 mm/hr except in June, one of the warmest months.

Mean air temperatures when the animals were "out" were at no time greatly different from those when they were "in" the water. The slightly lower temperatures when they were out in January-February apparently were related to the greater sky cover (= less insolation); the higher temperatures when they were out in March-April apparently were related to the lesser sky cover (= greater insolation). From May to July, air temperatures were not correlated with the amount of insolation, and in those months both animals continued to haul out in the sunnier weather but in slightly cooler air than when they were in the water. During sunny days in summer, when air temperatures rose to 25°C or more, they spent most of their time in the water, rarely hauling out for more than an hour at a time. They tended to haul out mostly at night in the warmest months. Though they apparently became acclimatized to a certain degree to the temperate climate, they consistently avoided exposure to the greatest solar and atmospheric heat by escaping to the water.

Activity in relation to weather: wild walruses. Our data from walruses sighted in the field are less extensive than those from the captives, but they also suggest an avoidance of high wind in cold weather, irrespective of the sky cover (Table IV). In January, all the animals sighted when winds were 4 mps (10 mph) or stronger were in the water, whereas most of those sighted during lower wind velocities were on the ice.

Winds up to 9 mps (20 mph) seemed not to deter the animals from hauling out in air at –7 to 6°C in May, even under overcast skies; indeed, in that month we saw more walruses on the ice in windy weather than when it was calm. In June at Round Island, also, most of the animals resting on a windward beach during a squall with 10 to 12 mps winds and rain (air 12°C) were little affected. Though they were appreciably more restless than they had been earlier in the day in more moderate weather, they showed no clear signs of withdrawing into the sea (10°C). The highest rate of emigration from the beaches of Round Island occurred during the warmest afternoon (air 14°C, wind 0 to 2 mps, sky clear), and we interpreted this as an indication of intolerance of excessive heat, mostly from intense solar radiation.

TABLE IV.
COMPARATIVE WEATHER WHEN FREE-LIVING WALRUSES WERE SIGHTED OUT *vs.* IN THE WATER NEAR ST. LAWRENCE ISLAND, BERING SEA.

Month	Animals Sighted		Air Temp. (°C)	Sky Cover	Occurrence of Precip.	Wind Velocity (mps)
	No.	% Out				
January	10	*0*	–27	clear	none	11-13
January	25	*0*	– 8	clear	none	9
January	11	*0*	–26	clear	none	4
January	3	*33*	–23	clear	none	0-2
January	25	*100*	–19	overcast	none	0-2
January	6	*100*	–12	overcast	none	0-2
January	25	*100*	– 3	overcast	snow	0-2
March	5	*0*	– 1	clear	fog	0-2
May	310	*97*	2,3	clear	none	4-7
May	418	*87*	1,2	clear	none	2-4
May	96	*44*	–2 to 2	clear	none	0-2
May	58	*98*	–7 to 2	overcast	none	4-9
May	58	*95*	–2 to 6	overcast	none	2-4
May	261	*90*	–5 to 3	overcast	none	0-2
June	3	*0*	4	clear	none	0-2

Discussion

The physical environment of pinnipeds comprises parts of both the hydrosphere and the atmosphere, with, in some cases, nearly equal amounts of time spent in each. The aquatic portion is usually the more uniformly cold and stable; the atmospheric portion is relatively unstable and heterogeneous and, at times, can be either colder or warmer than the sea. The homeotherm that inhabits both must possess unusual thermoregulatory versatility. Reports from many sources make it clear that this requirement is met in pinnipeds not only by physiological means but by extensive behavioral adjustments as well. For example, in cold or stormy weather, northern fur seals, *Callorhinus,* huddle together or withdraw into the sea (Bartholomew & Wilke, 1956; Fay, unpublished); Weddell seals, *Leptonychotes,* seek sunshine and shelter from the wind (Smith, 1965; Ray & Smith, 1968); gray seals, *Halichoerus,* avoid snow-covered surfaces (Waters, 1965), and Steller sea lions, *Eumetopias,* remain in the water (Kenyon & Rice, 1961). In warm weather, fur seals, *Callorhinus* and *Arctocephalus,* seek shade and moisture, expose areas of bare skin, and fan with their flippers (Bartholomew & Wilke, 1956; Paulian, 1964); monk seals, *Monachus,* make wallows in the damp sand or lie in the shade of a bush or cave (Kenyon & Rice, 1959; van Wijngaarden, 1962); elephant seals, *Mirounga,* and South American sea lions, *Otaria,* may escape the heat altogether by staying in the water (Laws, 1956; Vaz-Ferreira & Palerm, 1961). Some of these tactics may considerably extend the thermal comfort zone well beyond the capacity of physiological mechanisms alone; others, such as escape into the water, indicate that the limits of the comfort zone have been exceeded.

We assume that adult walruses, like other polar pinnipeds (Irving & Hart, 1957; Davidov & Makarova, 1964), are fully adapted for thermoneutral existence in icewater, even while at rest, for they spend the greater part of their life there and may remain immersed for several days or weeks at a time. They are capable of sleeping in the water and frequently do so, yet at certain times they seem more inclined to rest in air than in the ostensible comfort of the sea. While out of the water or in anticipation of hauling out, they are notably selective of weather conditions, generally seeking exposure to sunshine and avoiding exposure to high winds and precipitation. In addition to their selection of the more favorable thermal conditions, usually warmer than the sea, they employ heat-conserving behavior in all but the warmest weather. The usual result is a relatively high, stable temperature in the skin and appendages (Ray & Fay, 1968), and we think that this is the principal benefit derived from hauling out. The tissue most affected by it is the epidermis, the outermost layer of the skin. Whereas, it is about as cold as the water during immersion, it can become 30°C warmer following emergence. Since epidermal mitosis in pinnipeds probably occurs only at relatively high tissue temperatures (Feltz & Fay, 1967) and, perhaps, only when the animals are inactive or asleep (Bullough, 1962; Bullough & Rytömaa, 1965), growth and regeneration of the skin, as in the molt and healing of wounds, may be feasible only when the animals are at rest out of the water. This is not a new theory (Laws, 1956; McLaren, 1958), but it is presented here in a new context, with new support. We feel that it could help to explain the conservative, thermophilic behavior of walruses and other polar pinnipeds when in air, in contrast to their apparent comfort in the usually colder sea.

The principal behavioral adjustments of walruses that favor the conservation of body heat when at rest in air are huddling, fetal posture, and basking in the sunshine. Huddling may have special significance for the calves, which possess less than half as much physical insulation (hair and blubber) as other arctic pinnipeds of comparable size. For the first two or three months after birth, thermal compensation for their deficiencies seems to be derived principally from contact with their mother ("brooding"). We consider brooding by walruses as the behavioral analogue of the woolly coat of young phocid seals, in that it provides warmth and insulation for the young animals while their blubber layer is developing (Davydov & Makarova, 1964; Ray & Smith, 1968). The young walrus also remains mostly in the atmosphere during this critical period, and the mother remains there with it. On many occasions, we observed that the cows with very young calves were extremely hesitant to take the calves with them into the cold water when threatened by hunters, whereas those with older calves showed virtually no hesitancy at all.

The huddling of adult walruses at rest has been recognized in a general way for a long time, but its potential contribution to thermal economy evidently has not been considered before. Among the Pinnipedia other than walruses, gregariousness is common during the pupping, mating, and molting periods, but huddling is uncommon. It seems significant that the walrus, the most polar of the otarioid seals and the most sparsely haired of all the pinnipeds, is also the most thigmothermal. By extensive mutual reduction of surfaces exposed to the cold air and substrate, the huddling walrus herd becomes a

heat-exchanging and heat-conserving unit with an advantage for arctic living. However, the persistence of thigmotactic behavior under all thermal conditions may place a limit on the amount of climatic heat that can be tolerated. Huddling is disadvantageous in warm weather, for it severely obstructs the dissipation of heat from the body.

By changing posture, the walrus is capable of regulating the amount of exposed surface and, thereby, of controlling the rate of heat loss. In contrast to huddling, posture is adjusted according to the ambient thermal conditions. The fetal posture (minimal exposure of surface) is clearly a reaction to cold that has potential value for conservation of body heat, whereas sprawling, with extension of the appendages, undoubtedly helps to accelerate cooling by exposing the greatest surface area for dissipation of heat. When very warm, walruses increase the convectional heat loss from their body by fanning, usually with one or both of the foreflippers. These are small relative to body size but have a large surface-to-volume ratio and can accommodate a large volume of blood probably at a high flow rate. The capacity of the hind flippers for transferring heat to the environment is enhanced also by evaporation when they become wetted by the animal's watery excrement. We frequently noticed also that the fore and hind flippers were damp in the absence of any extrinsic supply of moisture, but we were unable to determine the source of the dampness. Sweat glands were not found in any tissues from the bare flippers, though they were abundant in skin from the hairy parts of the body (Fay, unpublished).

Basking is another effective means for conserving body heat, largely by acquiring heat from solar radiation. We assume that the dark surface of the walrus' body absorbs radiant heat about as well as a black body, and that the short hair serves to retain it somewhat better than a bare surface. The hair may function also as a baffle, protecting against excessive convectional heat loss in all but the windiest weather.

Walruses in captivity at mid-latitudes showed an affinity for sunshine from March to July but tended to avoid prolonged exposure during the warmest months, when the insolation was about twice as strong as that in their native habitat. The calves were more inclined to expose themselves to it than were the juveniles, perhaps because of their smaller size and less effective thermoregulatory system. However, we observed, as did Reventlow (1951), that their greater exposure seemed to be the cause of a granular condition of the skin, tentatively identified as solar keratosis (cf. Mackie & Mackie, 1963). This occurred during the molt, in June, after the hair was shed and the skin was unprotected from the direct rays of the sun. In our animals, an acne-like condition often occurred with it, possibly due to blockage of the sebaceous ducts by an excess of keratin (van Scott, 1959).

The ultimate behavioral response to thermal conditions of the atmosphere is withdrawal into the water ("escape"). With increasingly cold weather, escape is preceded by the extreme fetal posture and intense shivering; with increasing warmth, it is the normal successor to sprawling and fanning. We believe that the range of conditions under which escape does not occur includes but slightly exceeds the "comfort zone." That is, we think that escape is not induced until the animals become uncomfortably hot or cold. Walruses that were acclimated for a year or more to the temperate climate of New York showed the escape reaction mostly when air temperatures were lower than 0°C or higher than 25°C, given sunshine, light winds, and a wet concrete substrate on which to rest. Newly captured calves, on a dry, wooden substrate in shade, were comfortable in still air only at temperatures between 5 and 18°C, and even after acclimation to warm weather in New York for 2 weeks, they tended not to lie out in air warmer than 20°C. Wild adults on ice may occasionally tolerate air as cold as −35°C with strong winds (Freuchen, 1935), but in our opinion, this is more the exception than the rule. Whereas the majority of those seen by us were on ice when air temperatures were higher than −20°C with little or no wind, nearly all were in the water when the air was colder or the winds were stronger. The upper threshold of air temperature that induces wild adults to escape or remain in the water seems to be between 10 and 15°C, given sunshine, light winds, and a damp, rocky substrate or ice.

Summary and Conclusions

1. The influence of climate on the distribution of walruses was investigated by observing their behavioral reactions to weather in the natural arctic and subarctic environment and in the temperate climate at the New York Aquarium. Walruses spend a large proportion of their time out of the water and are, therefore, exposed to conditions of the atmosphere nearly as often

as to those of the hydrosphere. Whereas they can sleep in the water in apparent comfort, they usually haul out on ice or land to sleep, especially during the spring and summer.

2. When at rest out of the water, they are highly gregarious and tend to huddle together at all times. This mutual reduction of exposed surface is advantageous for conservation of heat in cold weather, but it is a deterrent to their hauling out or remaining out when the weather is warm. Exposure of surface area is regulated also by the sleeping posture, which is adjusted for minimal exposure in cold and maximal exposure in warm weather.

3. Walruses are most active in the water at night and generally haul out to rest in the daytime. In doing so, they usually seek exposure to sunshine and avoid high winds and heavy precipitation. Their tolerance of wind and precipitation increases with rising air temperatures and increasing insolation, while their affinity for sunshine seems to remain unchanged. However, they evidently cannot tolerate for long the intense solar radiation in summer at mid-latitudes, and the young may be adversely affected by it.

4. The principal benefit derived from their hauling out to sleep seems to be the warming of their peripheral tissues, which may require heat and physical inactivity to fulfill their growth and reparative functions. Sustained warmth of the skin and appendages may be especially important for the molt, healing of wounds, and the development and survival of the newborn young.

5. When the weather is excessively cold or hot, the animals withdraw into the relative comfort of the sea after brief exposure or refrain from hauling out altogether. Thus, the upper and lower limits of their thermal tolerance are recognizable from this escape reaction. These limits may be expected to vary seasonally and, perhaps, with age, sex, reproductive status, health, and individuality.

6. The average limits of thermal tolerance of adult Pacific walruses while at rest in air seem to be between −20 and +15°C, given light winds, moderate insolation, and a cool, damp substrate on which to lie. Colder and warmer conditions may occasionally be tolerated, but only for short periods.

7. The highest air temperatures and most intense insolation received in coastal areas at the southern edge of the Pacific walrus' present range tend to induce the escape reaction. Warmer conditions, such as are found farther to the south, could be expected to discourage them to a greater extent from hauling out during the day in the spring and summer months, when they would ordinarily spend the most time out of the water. We feel that the conflict with their normal feeding, molting, and calving schedules could be sufficient to deter them from extending their range southward under present climatic conditions.

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EXPLANATION OF THE PLATES

PLATE I

FIG. 1. Herd of adult female walruses resting on an ice floe off Cape Lisburne, Alaska, summer, 1937. Photo by M. Woodbridge Williams.

FIG. 2. Herd of male walruses resting on Round Island, Bristol Bay, Alaska, June 27, 1958. Photo by Karl W. Kenyon.

PLATE II

FIG. 3. Walrus calf resting in "fetal" position with near minimum exposure of body surface. New York Aquarium, June 18, 1961.

FIG. 4. Same calf, a few minutes later, in sprawling position with near maximum exposure of body surface and appendages. Note huddling calves in background.

PLATE III

FIG. 5. Adult female walrus sleeping in the "semifetal" position. St. Lawrence Island, Alaska, May 16, 1959. Air temperature at the time was 3.5°C, the wind about 7 mps, and the sky was clear.

FIG. 6. A group of male walruses that had recently emerged from the water, Round Island, June 27, 1958. Note fetal posture of the animal at center. Air temperature 13°C, wind 1 mps, sunny with a high, thin overcast. Photo by Karl W. Kenyon.

PLATE IV

FIG. 7. Herd of male walruses resting in the afternoon sun, Round Island, June 24, 1958. Note the animal sprawled on the rock at center and the abundance of outstretched flippers, many of them fanning (arrows). Air temperature 14°C, wind about 1 mps, sky clear. Photo by James W. Brooks.

FIG. 8. Two male walruses resting in the sprawling posture with flippers extended and spread, Bering Strait, May 18, 1963. The animal at left was fanning. Air temperature 8.5°C, wind calm, sky clear. Photo by John J. Burns.

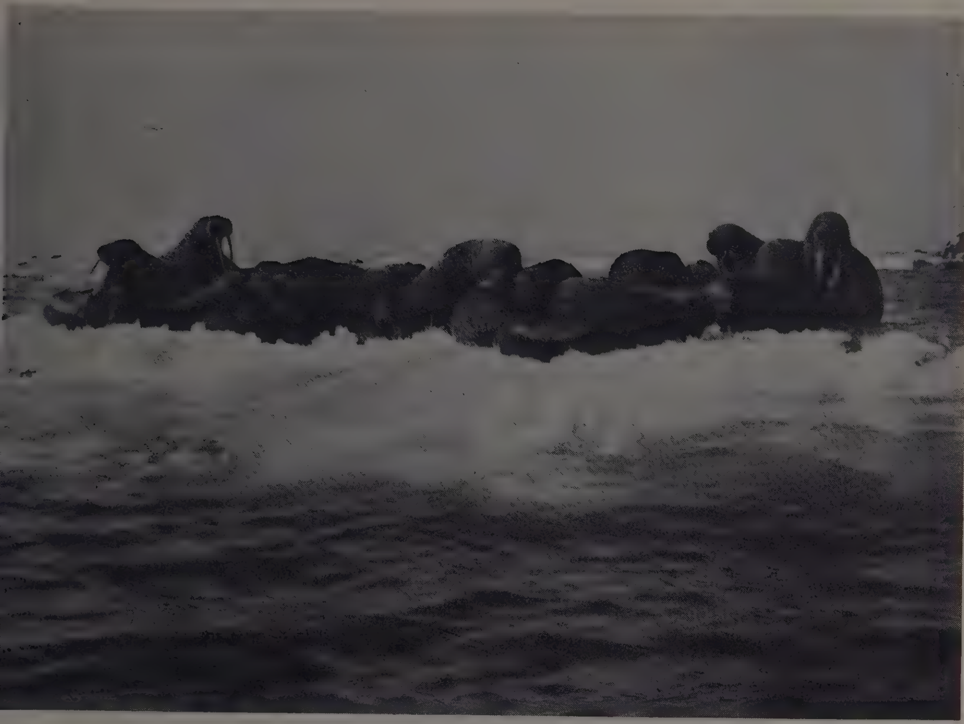

FIG. 1

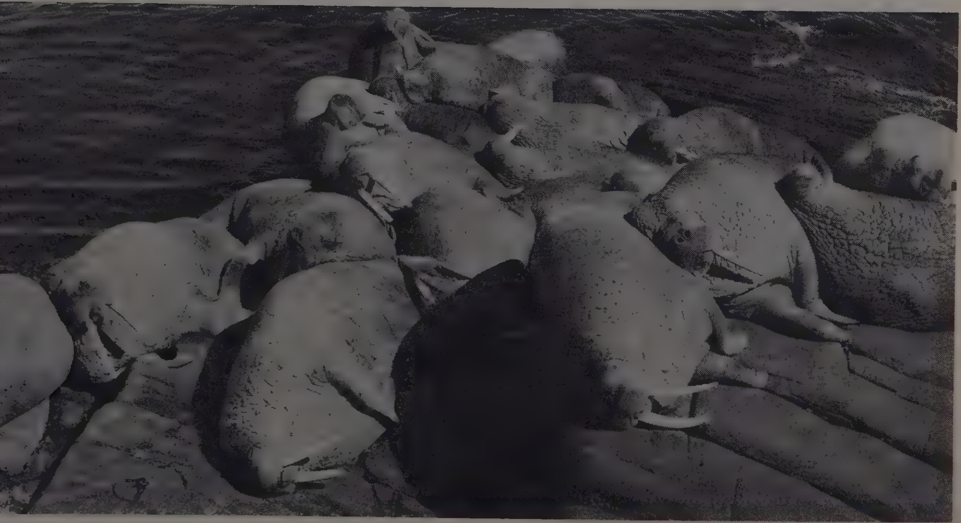

FIG. 2

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, ODOBENUS ROSMARUS (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.

FIG. 3

FIG. 4

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, ODOBENUS ROSMARUS (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.

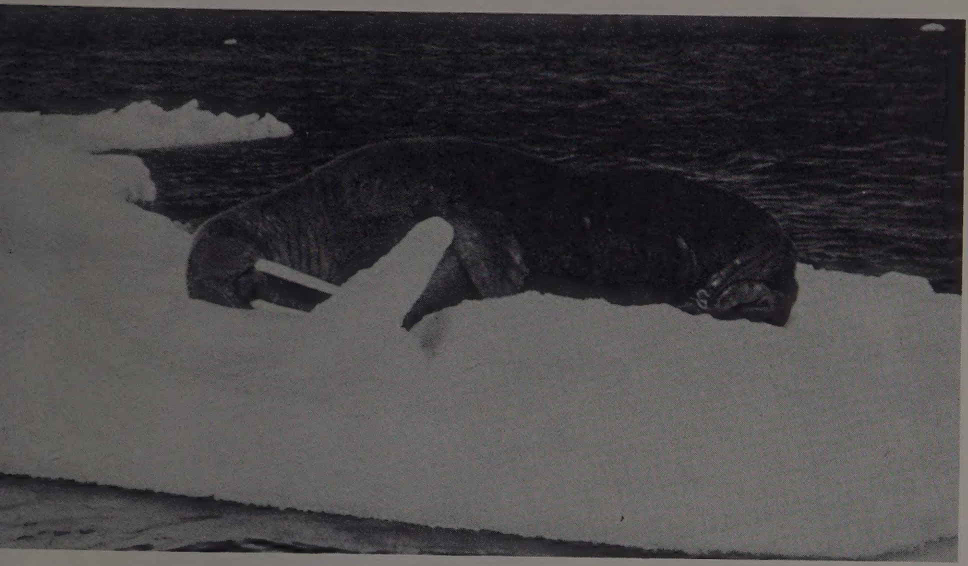

FIG. 5

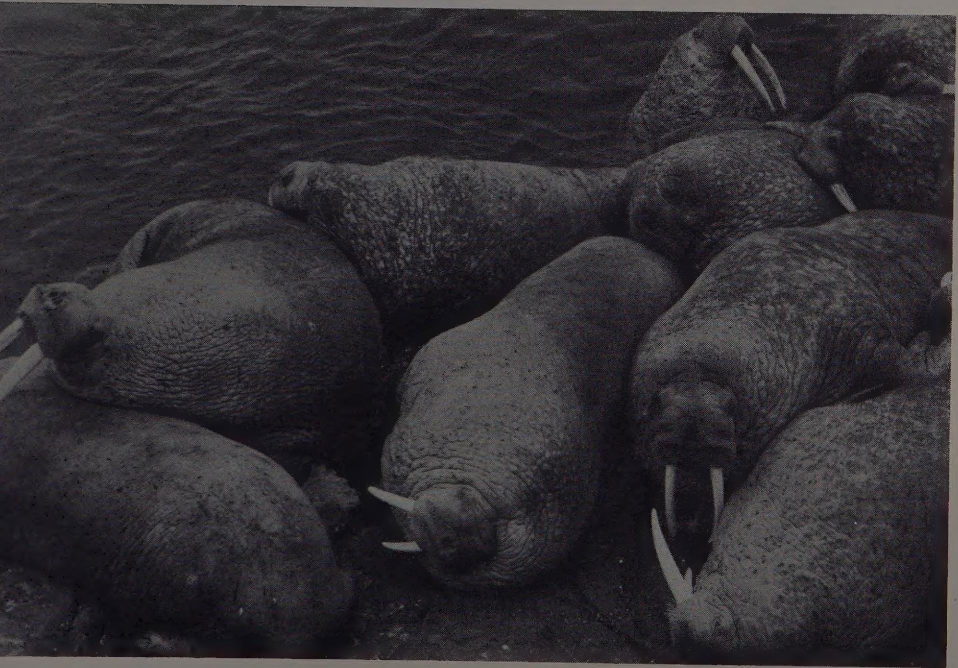

FIG. 6

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, ODOBENUS ROSMARUS (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.

FIG. 7

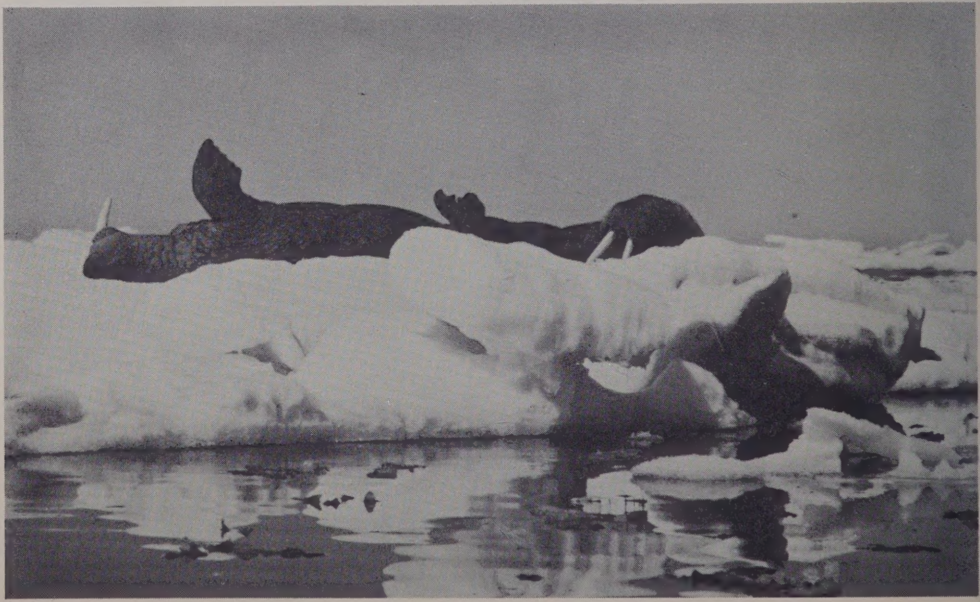

FIG. 8

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, ODOBENUS ROSMARUS (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.